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ON THE EYES OF TSETSE FLIES

By H. Eltringham, D.Sc., F.R.S.

[Read 3rd June, 1936.]

With Plate 1.

I regret that so long a time has elapsed since I received the first consignment of Tsetse flies from Dr. C. H. N. Jackson then working on the eastern shore of Lake Victoria. Sections were made from much of this material, but many unforseen circumstances have delayed the working out of the structures. It has been suggested that the Tsetse fly must have exceptional sight, since it appears to recognise possible prey from considerable distances, and as it will attack rough models of animals, the factor of scent seems much less important than in some other Diptera which are attracted by the odour of their food or breeding-places.

The first difficulty to present itself was the scarcity of works on the eyes of Diptera. It was not possible to decide whether the eyes of *Glossina* were peculiar, in the absence of comparable data concerning other forms. I am indebted to the Registrar of our Society for obtaining a copy of Dietrich's paper on the eyes of Diptera (Dietrich, W. 1909, *Die Facettenaugen der Dipteren*, Leipzig).

Later I received a consignment of flies from Dr. T. A. M. Nash of the Gadau Research Station in Northern Nigeria, and my histological investigation of this material suggested some further measurements which I could no longer carry out on the east African forms, as I had used up all the available examples. Before this paper is published, however, I hope to have further material from east Africa.

Technique.

Eyes are always difficult subjects for sectioning owing to the hardness of the cornea and other parts of the head. The material was preserved for the most part in Picro-chlor-acetic acid. Some examples were dehydrated in acetone, soaked in benzol, and thence transferred to paraffin. By far the most perfect embedding was, however, obtained by transferring from about 70% alcohol, in which the preserved heads were washed, to a fluid called Solvax, supplied by Messrs. Flatters & Garnett. This medium acts in much the same way as Cellosolve, but is cheaper. It will dehydrate from 20% alcohol and mixes easily with paraffin. Material should be transferred from solvax (in which it may have remained overnight) to melted paraffin, and after about 15 minutes removed to fresh paraffin. After 10 to 15 minutes in this, it is ready for cooling and embedding.

The rapidity of this process and consequent short exposure to heat, combined with the absence at any stage of strong alcohol, minimises the hardening of the chitin. The comparative absence of shrinkage as compared with examples subjected to strong alcohol and prolonged heat, is very marked.

The stains used were Iron-Haematoxylin, Mann's stain with Dobell's differentiation, and Mann's stain combined with momentary immersion in alcoholic Light Green. For undepigmented material Light Green alone is very effective for demonstrating the arrangement of the pigment. Depigmentation was effected with Grenacher's fluid.

The eyes of Diptera present many forms. Some are double, the facets of one half being larger than those in the other. This difference in size of facets may be graduated from one part of the eye to another. There may be much diversity of the finer structure of the ommatidia, and in the convexity, external or internal, of the corneal lenses. The great majority are of the pseudocone type, though even this feature is not universal, since the eyes of TIPULIDAE are of the Acone type, and of a peculiar form described long ago by Grenacher, and re-illustrated in my *Senses of Insects*, p. 28. I know of no Dipterous insect possessing either Eucone or Exocone eyes, and one must therefore assume that such images as their eyes are capable of forming are of the apposition type. Descriptions of the different forms of eyes and their images will be found in the above work, but it may be useful here to recall that in the Pseudocone eye the light is concentrated by the corneal lens on to the wide end of the pseudocone. Actually a small inverted image is here formed, but as an image it is of no value, since the pseudocone cannot re-invert it (as the eucone does) but merely further concentrates the light on to the rhabdom, which is surrounded by the visual cells or retinulae. Thus the image of the whole field is made up of minute dots of light each of the average value of the light coming from that part of the field towards which the facet is directed, and resembles a half-tone print, which is also made up of dots. The gradation in such a print is, however, obtained by differences in the sizes of the dots, whereas in the pseudocone image it is composed of dots of the same size but of different light intensity, and should therefore be slightly superior when the same number of dots are employed.

The structure of the eyes of the different species of Tsetse that I have examined does not greatly vary either in the species or the sexes, and a detailed description of one species will suffice for an understanding of the arrangement.

Plate 1, fig. 1, shows a section through an eye of *G. tachinoides* cut in a plane at right angles to that of the expanded wings. It is possible to obtain a section in this plane, in which all the facets are of about the same size, as shown in the illustration. The outer surface of the cornea is very regular, and the lenses nearly flat externally. Their inner surfaces are, however, markedly convex. Beneath each lens lies the pseudocone which consists of a thin sheath, containing an apparently fluid substance which disappears in the course of preparation. There is one rather curious feature in which the pseudocones of some species of *Glossina* differ from those of other eyes of Diptera. Extending from the common centre of the retinulae at the apex of the pseudocone, to the centre of the proximal side of the corneal lens, is a rod- or thread-like structure, which in transverse section under a very high magnification can sometimes be resolved into four strands. Morphologically it is probably the remains of the inner walls of the four primitive cells from which the pseudocone is formed. It is very conspicuous in sections of *tachinoides* and *submorsitans*, but obsolescent or absent in *palpalis*, *pallidipes*, and *swynnertoni*. Whether it has any mechanical or optical significance would be difficult to decide, though as some species of similar habits get on very well without it, it is probably a purely morphological feature.

The whole eye is heavily pigmented, the colour in all species examined being red. The actual number and arrangement of the pigment cells is difficult to decide and is not of great importance, but pigment granules are extremely dense round the pseudocones and round all the tracheal vessels. At fig. 4 I have shown diagrammatically two elements of the eye of *tachinoides*, though it should be understood that the proximal parts are rarely so regular as there

shown owing to the tracheal displacement of the retinulae. At the apex of the cone the retinulae are swollen into a kind of knob containing four nuclei, probably the nuclei of the four primitive cells. Dietrich notes this arrangement in the species of Diptera he examined and calls the four divisions at the head of the retinulae "crystal cells." He further states that the rhabdomeres, or separate edges of the retinulae, are extended into the crystal cells and usually take a dark stain. This feature is observable in *palpalis*, but not in *tachinoides* or *submorsitans*. The number of retinulae in each ommatidium appears to be six, though in some sections a seventh can sometimes be resolved. Dietrich claims to have observed in some of his species a rudimentary eighth retinula, recognisable by its nucleus.

The primitive number of retinulae in compound eyes seems generally to be eight, though one, and sometimes two, may be only rudimentary. In most of the Diptera examined by Dietrich, seven retinulae are described, and the seventh projects into the central lumen in an asymmetrical fashion. This feature is not specially observable in *Glossina*, though something of the kind can be seen in a few sections. Just beneath the pseudocone apex the retinulae are contracted to a narrow neck and then diverge again to form a rather thick rod, the centre of which is the rhabdom, formed from the inner contiguous edges of the retinulae. The light is supposed to pass down the rhabdom and stimulate the retinulae throughout their length. On reaching the basal membrane the retinulae are fined down to slender nerve threads which pass into the outer optic ganglion, the periopticon. At the level of the basal membrane there is a very heavy layer of pigment. In a transverse section at this level, of an eye of *palpalis*, fig. 7, the pigment being intact and the plasma stained light green, the nerves can be very clearly seen, and are, in nearly every element, seven in number, though at more distal levels of the eye only six retinulae can be counted. It would appear that the seventh nerve does not extend to the more distal levels of the eye. In similar sections of an eye of *tachinoides* I have sometimes been able to count eight nerves, so that the primitive eighth is still occasionally present in the proximal part of the eye.

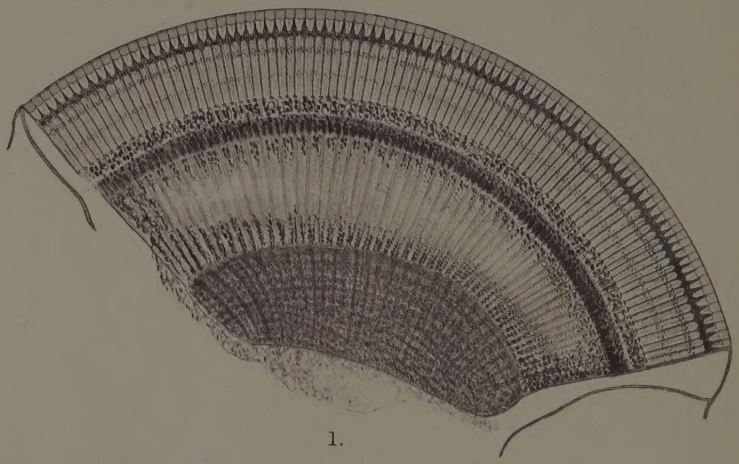
Just distal to the basal membrane the tracheal vessels are much distended, thus reducing the bundles of retinulae to very slender dimensions. This feature is carried to a maximum in SYRPHIDAE. Dietrich suggests that their function is to isolate the elements of the eye by total reflexion, and also to increase the size of the eye without altering the centre of gravity. The latter suggestion seems to me rather improbable.

At fig. 5 is a series of transverse sections of an ommatidium. *a* to *e* are taken from preparations of *tachinoides*. *a* is the pseudocone where it joins the corneal lens, and the rod-like structure can be seen in the centre. *b* is a little farther down where the more or less radiate substance of the pigment cells can be seen surrounding the pseudocone. *c* is at the level of the pseudocone apex, *d* a little further down showing the six retinulae, and *e* still more proximal showing the tracheal vessels. *f* is a section of the proximal part of an ommatidium of *palpalis* to show the large proportional sectional area of the tracheal vessels. Fig. 7 is a section of an ommatidium of *palpalis* at the level of the basal membrane showing the seven nerve threads which pass to the external optic ganglion.

A marked feature of all the eyes examined is the variation in the size of the facets, coupled with a corresponding difference in that of the pseudocones, and of the lengths of the ommatidia. If a section be made at right angles to the plane of the expanded wings, as in fig. 1, any given section will show facets

of fairly uniform size. If, however, the section be made in the plane of the expanded wings, as in the diagram fig. 6, it is seen that the corneal lenses are larger in diameter and the pseudocones and retinulae longer as they approach the frontal region of the eye. Such differences are common in the eyes of Diptera, as already mentioned, and also in Odonata and some other insects. It is usually stated that larger facets are more adapted to recording movement than smaller ones, on the theory that greater contrasts are produced when a shadow moves from one facet to another, very small facets not producing such sharp changes. However this may be, I am inclined to think that larger facets provide for the admission of more light, and that this is probably the more important factor for the perception of movement. On the other hand, so long as the larger facets radiate from the same centre as the smaller, their sight will be less well defined. Insects are extremely short-sighted. A large number of facets must be engaged if the outline of the object is to be at all distinct, just as a "half tone" print is the finer when the dots formed by the screen with which the block was made are more numerous. When the corneal curvature is part of a sphere, the number of facets engaged in viewing a given object is inversely proportional to the square of the distance, and hence the number decreases with great rapidity as the object becomes more remote. Few corneae are, however, strictly spherical, and the flatter the cornea the longer will be the sight. Only rays nearly perpendicular to the facet will reach the retinulae, those striking it at any considerable angle being absorbed by the pigment surrounding the pseudocones. It is perhaps easier to think of the rays the wrong way round. Imagine rays emanating from the cornea. Where this is fairly flat, such rays will spread but little, but where it is sharply curved they will be rapidly dispersed. If the rays entering the facets be now thought of, those arranged on a short radius will pick up only widely scattered points of light from a moderately distant object and the distinctness of the image will be thereby impaired. With a flattened corneal surface the points of light from the object will be nearer together, and furthermore the separation will not increase with the same rapidity as the object becomes more remote. It will be seen from fig. 6 that the cornea has a much flatter curve in the front of the eye than at the sides, and it may well be that the anterior facets can see at least recognisably, for a greater distance than the lateral ones. If this be so, it would seem that the eye is well adapted, so far as a compound eye can be, to distinguish distant objects, and with these flies, one would expect the prey, as the distant object, to be in the "straight ahead" direction. It is true that other flies which appear to depend less on sight than on scent have similar eyes, but nothing whatever is known of the perceptive power of the insect brain, and certainly one cannot venture to gauge it by the structure of the dioptric apparatus. Even in ourselves there are great differences in perceptive power. Two persons with similar sight may "see" an object but only one of them perceive it. In a similar way, faint or obscure stimuli may guide a Tsetse fly to its prey, equal stimuli having little effect on the reflexes of other species of Diptera, though the latter may have very similar eyes. Other factors apart, the range and acuity of vision of which a compound eye is capable depend on the number of the facets. Thus the large Dragonflies seem to have the best sight, and they have the largest eyes and the greatest number of facets, though some of the SPHINGIDAE come very near to them in this respect.

At fig. 2 I have drawn an outline of the head of *Glossina submorsitans* taken from a cleared example of the head, and at fig. 3 a similar representation of the head of *G. tachinoides*. The much larger eyes of *submorsitans* are at once



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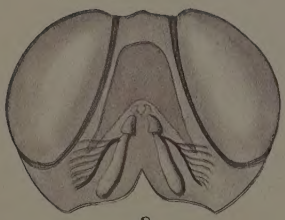

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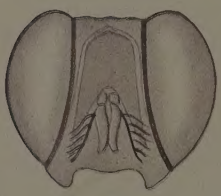

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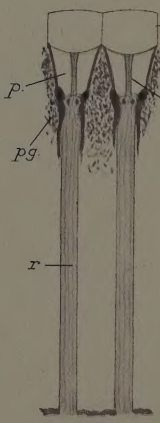

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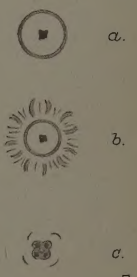

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THE EYES OF TSETSE FLIES.

evident. Dr. Nash states in a letter that *tachinoides* is a "thicket fly." It does not forage, but waits for its prey in the densest shade, whereas *submorsitans* is an open-country fly. The much larger eyes of *submorsitans* seem therefore to be an adaptation to its habits. It has many more facets, and apart from the factors of size and curvature, must have the better sight.

Description of Plate 1.

Fig. 1. Section of eye of *Glossina tachinoides* cut at right angles to the plane of the expanded wings.
2. Head of *G. submorsitans* to show relative size of eyes.
3. Ditto of *G. tachinoides*.
4. Two ommatidia of *G. tachinoides*. *l*, lens, *p*, pseudocone, *pg*, pigment, *cf*, central filament, *r*, retinulae.
5. *a* to *e*, Transverse sections of an ommatidium of *G. tachinoides*, *f*, section of an ommatidium of *G. palpalis* near basal membrane.
6. Diagram of section of head of *G. tachinoides* to show variation in size of facets and ommatidia.
7. Section of an ommatidium of *G. palpalis* at level of basal membrane, showing the seven nerve-threads.

Dimensions.

Maximum diameter of facets	·03 mm.
Minimum „ „ „	·015 mm.
Width of head of *submorsitans*	2·6 mm.
„ „ „ „ *tachinoides*	2 mm.